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Revision of *Agathodesmus* Silvestri, 1910 (Diplopoda, Polydesmida, Haplodesmidae)

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Abstract

Agathodesmus Silvestri, 1910 includes *A. baccatus* (Carl, 1926) **comb. n.** from New Caledonia, *A. bucculentus* (Jeekel, 1986) **comb. n.** from Queensland, Australia, and *A. johnsi* **sp. n.** and *A. steeli* Silvestri, 1910 (type species) from New South Wales, Australia. *A. baccatus* and *A. bucculentus* were formerly placed in *Atopogonus* Carl, 1926 **syn. n.** The identity of the apparently congeneric *Inodesmus jamaicensis* Cook, 1896 sensu Loomis, 1969 from Jamaica is still uncertain, and *Inodesmus* Cook, 1896 remains a nomen inquirendum.

Keywords

Diplopoda, Polydesmida, Haplodesmidae, Australia, New South Wales

Introduction

Filippo Silvestri (1910) erected the polydesmidan genus *Agathodesmus* Silvestri, 1910 for a single female specimen from Australia. Because millipede taxonomy is based largely on male genitalia, the classification of *Agathodesmus* and its type species *A. steeli* Silvestri, 1910 has been uncertain for almost 100 years.

Neither Silvestri (1910), nor Attems (1914, 1940) nor Brölemann (1916) assigned the genus to a family. Hoffman (1980) placed *Agathodesmus* in Dalodesmidae Cook, 1896 (suborder Dalodesmidea Hoffman, 1980) without explanation. On the basis of

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Silvestri's brief description of non-genitalic characters, Jeekel (1985) assigned *Agathodesmus* to Haplodesmidae Cook, 1895 (suborder Polydesmidea Pocock, 1887). Jeekel later qualified his assignment, saying that *Agathodesmus* was a "potential" haplodesmid, but in the absence of males "as yet no certainty can be obtained" (Jeekel 1986, p. 46). Simonsen (1990) also placed *Agathodesmus* in Haplodesmidae, while Golovatch et al. (2009), in a revision of Haplodesmidae, excluded *Agathodesmus* from the family, arguing that its type species was a nomen inquirendum, i.e. more information was needed.

In this paper I redescribe *A. steeli* from the holotype and from recently collected, nearly topotypical males and females. A second *Agathodesmus* species is described from a site ca. 180 km from the *A. steeli* type locality. The two species are shown to be congeneric with species of *Atopogonus* Carl, 1926 in Haplodesmidae.

Materials and methods

The type locality of *A. steeli*

Silvestri (1910) reported that the *A. steeli* holotype was collected by Thomas Steel at Avoca, New South Wales (see Appendix). No additional information is on the holotype slide label (Fig. 1). At the beginning of the 20th century there were three New South Wales places called "Avoca": one in the dry southwestern corner of the State, one in the highlands west of Wollongong and one on the coast near Gosford. The latter "Avoca" is today known as Avoca Beach.

Independent evidence that the type locality is the highlands Avoca comes from records concerning Thomas Steel (1858-1925). Steel was an industrial chemist and was based in Sydney from 1893 to 1918 (Carter 1926). In his spare time Steel was a field naturalist with a taxonomic interest in Onychophora and terrestrial flatworms; he donated many specimens to the Australian Museum in Sydney (G. Milledge, pers. comm.). The Museum's collection database lists earthworms, onychophorans, terrestrial flatworms, frogs, lizards and snakes collected by Steel between 1895 and 1908

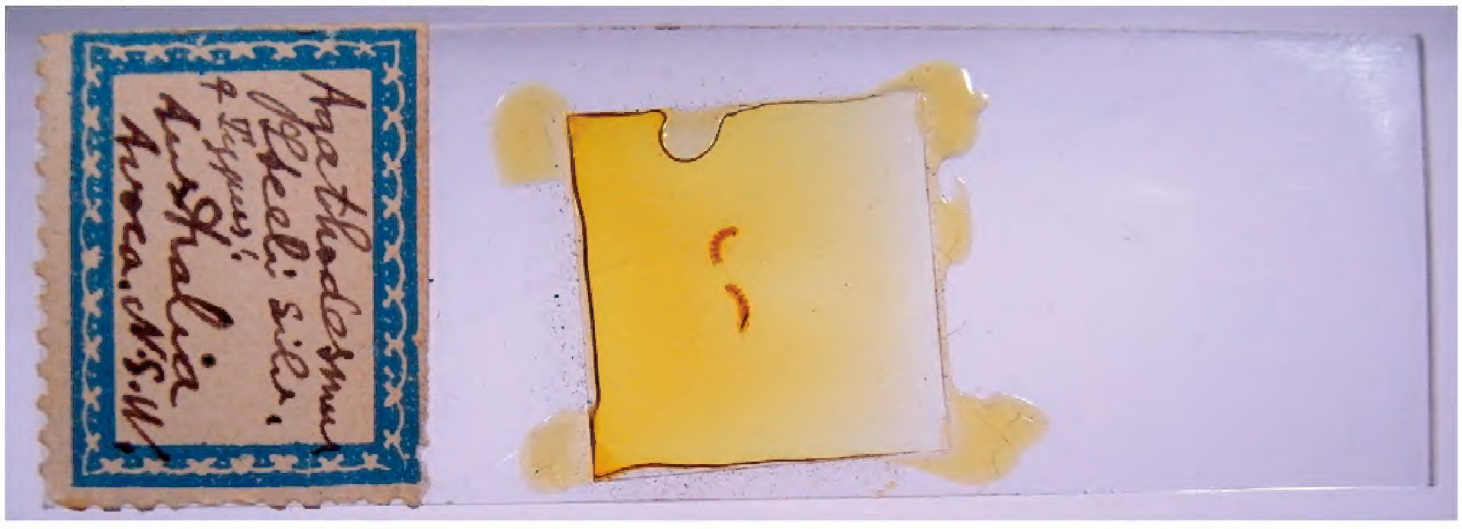

Figure 1. Holotype slide, photographed 1 May 2009. The label reads 'Agathodesmus / Steeli Silv. / ♀ Typus! / Australia / Avoca. N.S.W.'

from Bundanoon, Moss Vale, "Avoca, near Moss Vale", Wildes Meadow and Robertson. These five localities are clustered in the southern highlands of New South Wales (Fig. 2C). In Steel's time they were easily accessed by train from Sydney, and the area

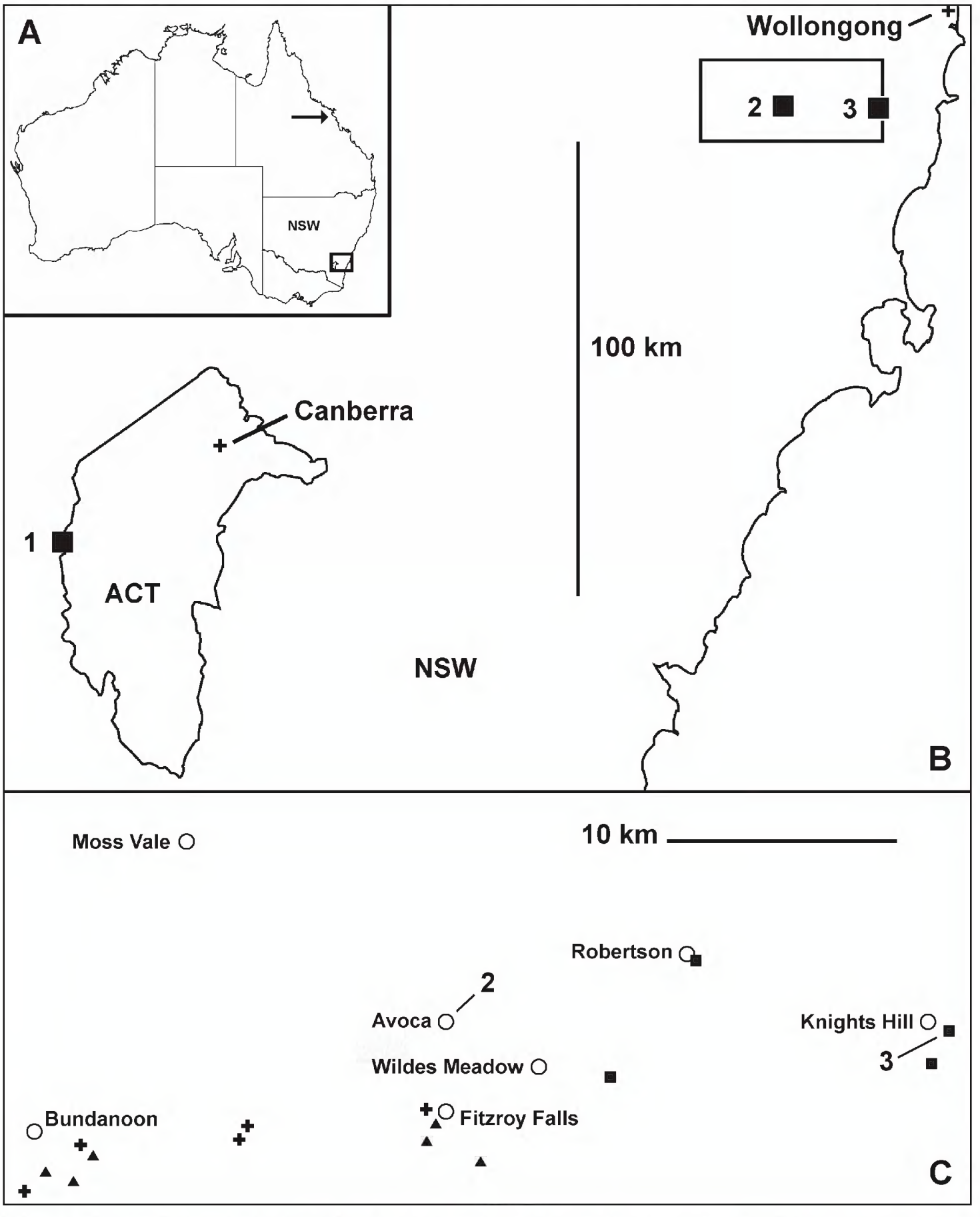

Figure 2. *Agathodesmus* localities. **A** Australia with rectangle indicating extent of map B; arrow points to type locality of *A. bucculentus*. **B** New South Wales localities (squares). 1 = Mt Aggie, *A. johnsi* sp. n.; 2 = Avoca, 3 = Knights Hill, *A. steeli* Silvestri, 1910; rectangle around 2 and 3 indicates extent of map C. **C** Southern highlands places (open circles), approximate sites for ANIC berlesates (triangles), 2009 search sites on sandstone and shale (crosses) and basalt (squares). Mercator projections.

had been popular with rail tourists since the 1880s (Garran 1886). There are no Steel collections in the Australian Museum from either of the other two "Avoca" localities in New South Wales (G. Milledge, pers. comm.)

The date of the *A. steeli* collection is unknown, but the Australian Museum collection database lists a terrestrial flatworm collected by Steel at Avoca in February 1905, and a leech, an onychophoran and flatworms collected by Steel at Avoca in January 1907. Both dates are consistent with the 1910 date for Silvestri's description. I have been unable to locate any correspondence between Steel and Silvestri, nor have I found any other information indicating how Silvestri acquired Steel's specimen.

Fig. 2C shows that Avoca (a named locality, not a town) is only ca. 4 km and 14 km, respectively, from the Steel localities Wildes Meadow and Moss Vale, and only 4 km from Fitzroy Falls, a tourist destination that was as well known by that name in Steel's time (Garran 1886) as it is today. It is likely, then, that the place name "Avoca" as used by Steel refers to a small area, perhaps only a few square kilometres.

2009 search for *A. steeli*

The Avoca locality today is cleared farmland on a small patch of Tertiary basalt (Fig. 9 in Bowie 2006). Although closed rainforest grew on basalt further to the east, the isolated Avoca basalt patch is thought to have carried open eucalypt forest, not rainforest, prior to clearing in the mid- to late 19th century (K. Mills, pers. comm.; Fig. 3.1 in Mills and Jakeman 1995). Thomas Steel may have collected *A. steeli* in an intact forest remnant at Avoca, or among logs and other woody residues of clearing operations.

On 6 and 7 April and 14 May 2009, I searched for *A. steeli* at the forested places near Avoca marked in Fig. 2C. I looked under stones, under loose bark on fallen trees, in and under rotting wood on the ground, and in fallen leaf and bark litter.

The five April sites carried open eucalypt forest on soils derived from shale and sandstone. These soils are relatively infertile and there is a large area of never-cleared forest on shale and sandstone south and west of Avoca. Spirobolida, Spirostreptida and paradoxosomatid Polydesmida were abundant at the five sites, with scattered occurrences of dalodesmid Polydesmida, Siphonophorida and Polyzoniida. I saw no Polydesmida in the *A. steeli* size range (ca. 6 mm long) other than early-stadium juvenile paradoxosomatids and dalodesmids.

The four May sites were all on basalt and carried either closed rainforest or tall eucalypt forest with a variably dense understorey of small trees. Uncleared forest on fertile basalt soil is rare in the area, and the remnants I searched have survived largely because the ground under the trees is too stony for farming. The millipede fauna appeared to be the same at the basalt sites as at the sandstone and shale sites, but the dalodesmid *Orthorhachis christinae* Mesibov, 2008 was noticeably more abundant. I found 11 adults and four juveniles of *A. steeli* in a single rotting log in eucalypt forest at Knights Hill, ca. 20 km east of Avoca. No other small, adult Polydesmida were seen at the basalt sites.

Other specimens

The Australian Museum in Sydney holds many millipede samples from New South Wales, mostly sorted to order or below. As part of a paradoxosomatid mapping project in 2006-07 (Mesibov 2008), all samples sorted to Polydesmida were examined by Cathy Car (Charles Sturt University) or myself. We sorted these further to Dalodesmidae, Paradoxosomatidae and "other". Among the latter samples I found specimens of a second *Agathodesmus* species collected in 1966 from the Brindabella Ranges west of Canberra, at a site ca. 180 km west and south of Avoca (Fig. 2B).

The Australian National Insect Collection in Canberra holds a small number of unsorted samples obtained from Berlese extraction of forest litter from the area I searched (Fig. 2C). I examined these samples but found no *Agathodesmus*.

Note on geography

The new *Agathodesmus* species described below was found on the summit of Mt Aggie. According to the Australian Museum database, Mt Aggie is in the Australian Capitol Territory, which is embedded within the much larger Australian state of New South Wales (Fig. 2B). The Commonwealth of Australia gazetteer (searchable online at http://www.ga.gov.au/place-name/) locates Mt Aggie in both the Australian Capitol Territory and New South Wales, because the mountain straddles the border between the two, and the border crosses the summit. The new species undoubtedly occurs on both sides of the border on Mt Aggie, and for practical reasons is here regarded as a New South Wales species.

Specimen treatment

"Male" and "female" in the text refer to stadium VII individuals unless otherwise indicated. Specimens are stored in 80% ethanol in the Australian Museum. Some specimens were cleared in 80% lactic acid, then temporarily mounted in 60% lactic acid for optical microscopy. SEM images were acquired digitally using an FEI Quanta 600 operated in high-vacuum mode; alcohol-preserved individuals and body parts were air-dried before sputter-coating with gold.

Abbreviations:

ACT	Australian Capitol Territory
AM	Australian Museum, Sydney
MCSN	Museo Civico di Storia Naturale "Giacomo Doria", Genova
NSW	New South Wales.

Results

Order Polydesmida Pocock, 1887
Suborder Polydesmidea Pocock, 1887
Haplodesmidae Cook, 1895

Agathodesmus Silvestri, 1910

Agathodesmus. Silvestri 1910:362. Attems 1914:282, 1940:487. Brölemann 1916:547,587. Jeekel 1971:310; 1982:11; 1983:146; 1985:50,51; 1986:46. Hoffman 1980:184. Simonsen 1990:57. Golovatch et al. 2009:2.

Atopogonus. Carl 1926:386. Attems 1940:477. Verhoeff 1941:406. Jeekel 1971:314, 1984:88, 1986:46. Hoffman 1980:186, 1999:480. Simonsen 1990:57. Golovatch et al. 2001:185, 2009:2,44. **New synonymy.**

Type species. *Agathodesmus steeli* Silvestri, 1910, by original designation; of *Atopogonus*, *A. baccatus* (Carl, 1926) **comb. n.**, by monotypy.
Other included species: *A. bucculentus* (Jeekel, 1986) **comb. n.**, *A. johnsi* **sp. n.**

Diagnosis. Small Polydesmida with head and 19 or 20 rings; body not curling in spiral; head and telson facing downwards; metatergites with numerous tubercles of different sizes, the largest sometimes bearing a single seta; ring 2 tergite extended laterally, basally and anteriorly, and edged with large tubercles; no paranota on posterior rings, sometimes replaced by short row of large tubercles just above leg bases; gonopod with neither cannula nor prostatic groove, telopodite consisting of more or less cylindrical basal portion with broad, flattened structure arising posterodistally on basal portion of telopodite and bent basally or basolaterally.

Agathodesmus steeli Silvestri, 1910
Figs 1, 3A-D, 4A-D, 5A, 5B, 6A-C, 7A

Agathodesmus steeli. Silvestri 1910:362. Attems 1914:283, 1940:488. Chamberlin 1920:137. Jeekel 1971:310, 1985:50. Golovatch et al. 2009:3.

Holotype. Female, permanently mounted on microscope slide in two pieces, with a break between rings 9 and 10 (Figs 1, 3A). Avoca, NSW, Australia, Thomas Steel, date not known. In MCSN.

Paratypes. None designated.

Other material examined. 7 males, 4 females, 1 stadium VI female, 2 stadium V females, 1 stadium IV female, Knights Hill, NSW, 34°37'07"S 150°42'38"E ±25 m, 720 m, 14 May 2009, R. Mesibov and T. Moule, wet eucalypt forest, AM KS107964 (three males, two females dissected).

Diagnosis. Head + 19 rings; gonopod telopodite with distal portion directed basally and slightly laterally near origin and with broad lateral branch apically expanded and divided into three anterobasally curving lobes.

Description. The original description (Silvestri 1910) is quoted in the Appendix. What follows is based on my examination of both the holotype and the Knights Hill material.

Adult with head + 19 rings (Fig. 4A). Live and freshly preserved adults pale with faint reddish pigmentation dorsally; in some individuals, pigment concentrated in transverse band at rear of metazonite. Male/female approximate dimensions: length

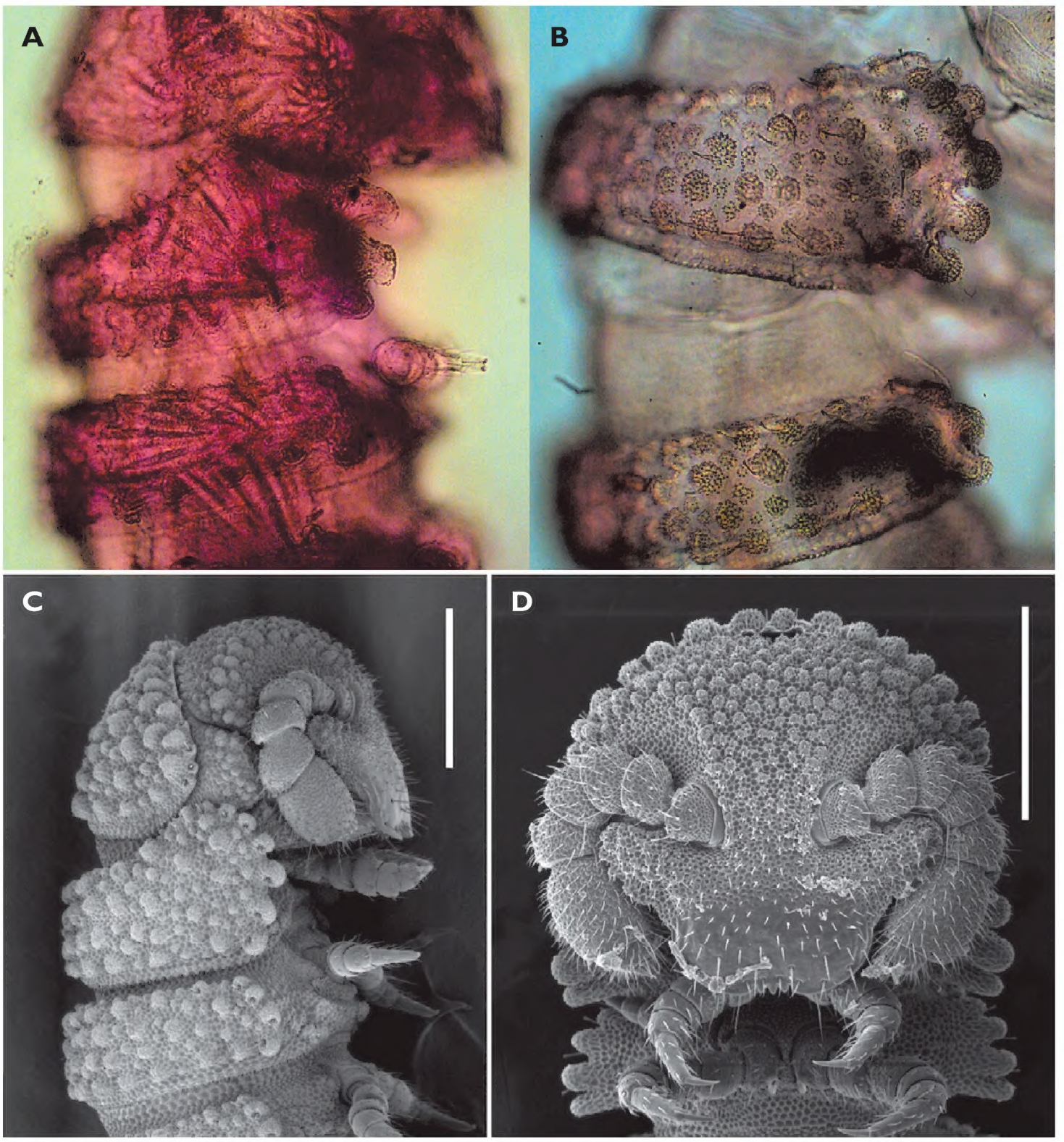

Figure 3. *Agathodesmus steeli* Silvestri, 1910. **A**-**C** Right lateral views of anterior end; **A** female holotype, **B** female (cleared specimen), **C** male. **D** Male, ventral view of head. **B**-**D** ex AM KS107964. (A), (B) to same unknown scale; scale bars in (C), (D) = 0.25 mm.

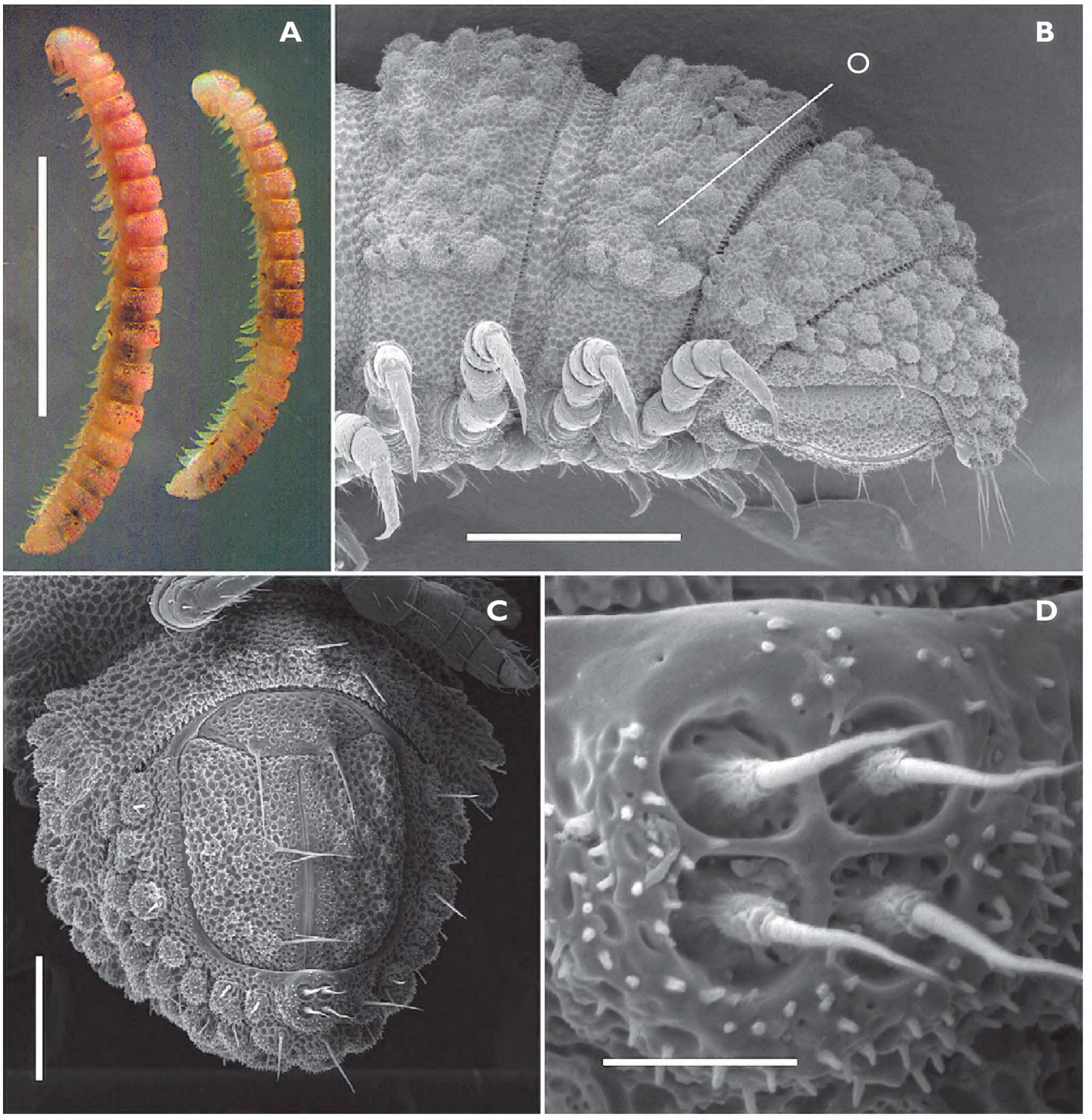

Figure 4. *Agathodesmus steeli* Silvestri, 1910, ex AM KS107964. **A** Female (left) and male (right); red colour is imaging artifact. **B** Male, left lateral view of posterior end; o = ozopore area. **C** Male, ventral view of telson. **D** Enlargement of **C** showing spinnerets. Scale bars: (A) = 2.5 mm, (B) = 0.25 mm, (C) = 0.1 mm, (D) = 0.02 mm.

4.5/5.5 mm, maximum width with paranota 0.5/0.6 mm, midbody vertical diameter 0.4/0.4 mm. Head (Figs 3C, 3D) about as wide as collum, overall body width almost uniform, tapering only slightly posteriorly from collum. Head facing downwards (Fig. 3C), with clypeus, frons and ventral part of vertex almost parallel to substrate and only slightly convex. Antenna (Fig. 3D) short, stout, clavate, held close to head, antennomeres 2 and 3 lying in broad, shallow excavation on head; antennomere 6 widest and longest; antennomeres 2-5 about equal in length, decreasing slightly in diameter from 5 to 2. Collum with slightly convex anterior margin and broadly convex posterior margin; corners rounded (Fig. 3C). Ring 2 tergite largest, extending basally, later-

ally and anteriorly well below collum corner (Figs 3A, 3B, 3C). Ring 2 and 3 tergites edged with 5-6 and 4 large tubercles, respectively (Figs 3A, 3B, 3C); posterior rings, including apodous ring 18, with row of 4 large tubercles just above leg bases forming all or part of lateral extension of metatergite, the anteriormost tubercle smaller than the posterior 3. Prozonites sharply demarcated from metazonites (Figs 3C, 4B, 6C). Ozopore (Fig. 4B) very small, not raised, in small, non-tuberculated area just above middle of group of 4 larger tubercles forming lateral metatergal extension; pore formula 5, 7, 9, 10, 12, 13, 15-18. Sternites on diplosegments (Fig. 5A) longer than wide, not setose, with distinct longitudinal and transverse impressions. Legs short, stout; relative podomere lengths tarsus>(prefemur, femur)>(postfemur, tibia); claw large, about two-thirds tarsus length. Spiracles not evident. Telson facing downwards (Fig. 4B), anal valves parallel to substrate and almost flat. Hypoproct trapezoidal (Fig. 4C); spinnerets in square array (Figs 4C, 4D); spinneret setae with single, low sheath, each seta in deep, walled depression.

Integument richly and densely sculptured (Figs 3D, 4C, 5A, 5C, 6A-C, 7A, 7B). Most of body covered with cuticle raised in cellular mesh of narrow folds, often with minute bumps (adorned with even smaller bumps) at or near fold junctions. Integument raised further as tubercles (Fig. 6A) of varying sizes on head, collum, tergites, metatergites and telson, the largest tubercles forming paranotum-like extensions on posterior rings; tubercles and some other parts of integument with minute, finger-like projections (Figs 4D, 6A, 6B), often arising along 'mesh-cell' boundaries. Cell boundaries at rear of metazonite extended as lappets, forming secondary limbus above primary limbus of uniform, triangular elements (Fig. 6C). Setae of normal type on legs and some other surfaces; a bisegmented seta with flattened, expanded tip (Fig. 6B) on each 'paranotum' tubercle and in association with some dorsal tubercles.

Male with gonopore opening at tip of cylindrical projection about 1/3 the length of leg 2 coxa, arising distomedially on the coxa. First legs somewhat swollen (Fig. 3C), no other anterior legs enlarged; neither sphaerotrichomes nor brush setae on any legs. Leg 7 bases well separated; leg 6 bases slightly separated, with a pair of short, rounded projections between coxae. Gonopod aperture oval (Fig. 7A), rim a little raised laterally. Gonocoxae (Fig. 7A) occupying full width of aperture; tapering a little distally; with mesh-like integumental sculpture and without setae; firmly joined medially near distal end. Telopodite (Fig. 7A) short, compact, when retracted reaching leg 7 base; broadly joined to gonocoxa (Figs 5B, 7A); no trace of cannula or prostatic groove; no integumental sculpturing; divided into more or less cylindrical basal portion and flattened distal portion. Basal portion of telopodite with blunt, basally directed projection arising posteromedial to junction with gonocoxa; portion terminating in flat, rounded tab bending posteriorly; with a few short setae on basal half of posterior surface of portion and three large setae in a row on lateral edge of posterior surface of terminal tab. Distal portion of telopodite a large, flattened structure arising on posterior surface of basal portion of telopodite just below terminal tab; curving basally and slightly laterally; divided near base into narrow medial branch, flattened apically with minute, spine-like protrusions on posterior and medial surfaces, and much larger lateral branch, the latter

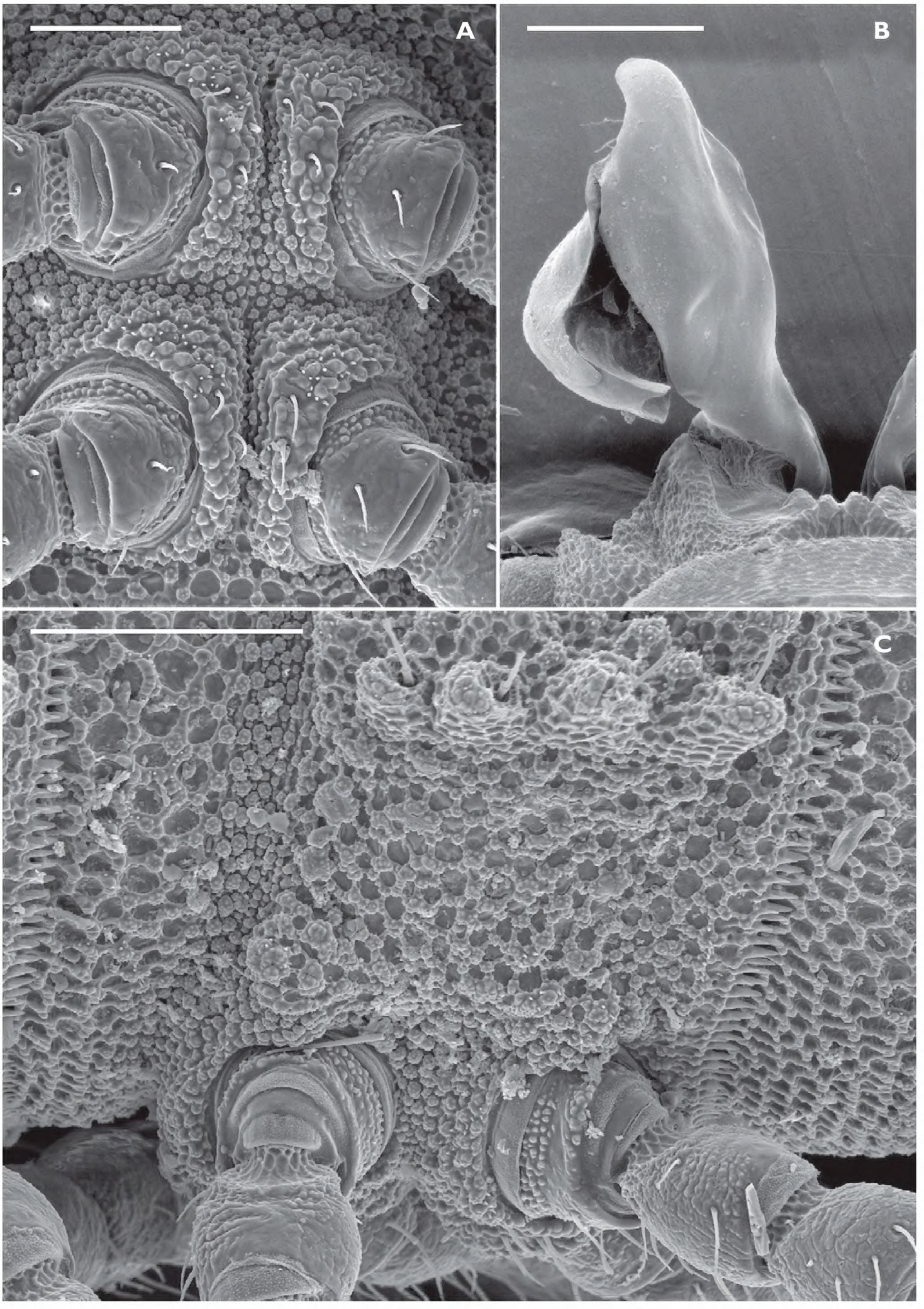

Figure 5. *Agathodesmus steeli* Silvestri, 1910, ex AM KS107964. **A** Male midbody sternite (anterior towards top). **B** Anterior view of extended left gonopod. *Agathodesmus johnsi* sp. n., ex AM KS94156. **C** Left ventrolateral view of male midbody ring (anterior towards left); no spiracles are evident above leg bases. Scale bars: (A) = 0.5 mm; (B), (C) = 0.1 mm.

much expanded, curving anterobasally and divided by two deep notches into three broad, rounded lobes (Figs 5B, 7A).

Female longer and more robust than male (Fig. 4A); epigynum inconspicuous, posterior margin barely raised; cyphopods not examined.

Distribution and habitat. Known so far from eucalypt forest (historically in the case of Avoca) at two localities ca. 20 km apart in southeastern New South Wales

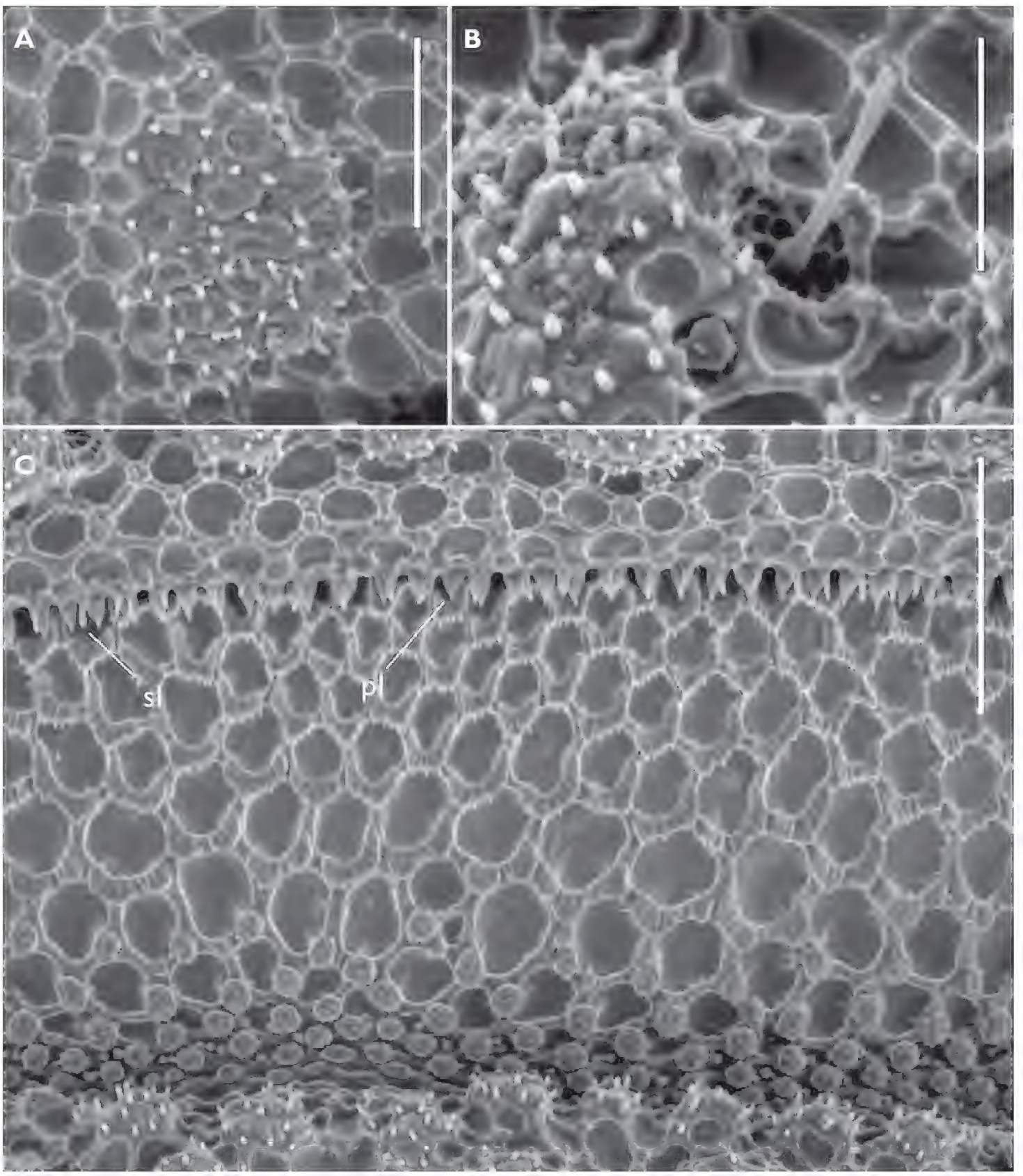

Figure 6. *Agathodesmus steeli* Silvestri, 1910, female ex AM KS107964. **A** Tubercle on midbody metatergite. **B** Bisegmented seta adjoining tubercle on midbody metatergite. **C** Dorsal view of midbody prozonite; limbus on next anterior ring at top, edge of metazonite at bottom; pl = primary limbus element, sl = secondary limbus element. Scale bars: (A) = 0.025 mm, (B) = 0.02 mm, (C) = 0.05 mm.

(Figs 2B, 2C). Both sites are above 700 m with annual rainfall probably >900 mm, in a temperate climate with cool winters. At the Knights Hill site, the 15 *A. steeli* specimens were found in narrow spaces in part of a large, moist, well-rotted log, either a *Eucalyptus* species or *Acacia melanoxylon*. Also in that part of the log were Siphonophorida, Symphyla, *Cryptops* sp. centipedes, fly and beetle larvae and terrestrial isopod crustaceans.

Remarks. Live *A. steeli* are very slow-moving and do not curl up, even when disturbed. Unlike adults of the morphologically, ecologically and behaviourally similar species of *Asphalidesmus* Silvestri, 1910 (Mesibov 2002, 2009), *A. steeli* adults are not heavily encrusted with soil particles.

The apparent absence of well-defined spiracles in *A. steeli* is remarkable. I have so far been unable to detect spiracles either with light microscopy (cleared specimens) or scanning electron microscopy (see also Fig. 5C). A histological study is needed to determine whether the tracheal system is also modified from the norm in Polydesmida.

Agathodesmus johnsi Mesibov, sp. n.

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Figs 5C, 7B

Holotype. Male. Mt Aggie, Brindabella Ranges, ACT, Australia, 35°27'S 148°46'E, 5000', 24 August 1966, P.M. Johns, snow sclerophyll, AM KS107965.

Paratypes. 12 males, 12 females, details as for holotype, AM KS94156 (two males dissected).

Diagnosis. Head + 19 rings; gonopod telopodite with distal portion directed laterally near origin and with broad lateral branch without notches, apically tapering and curving basally rather than anterobasally.

Description. Colour uniformly light yellow-brown after long preservation. Males and females as for *A. steeli* in all details so far noted, including apparent absence of spiracles (Fig. 5C), but male gonopod telopodite (Fig. 7B) with more short setae on posterior surface of basal portion, terminal tab narrower and less bent posteriorly, and distal portion directed laterally near base rather than posterolaterally, with narrow medial branch curving to lie against broad lateral branch, the latter undivided, curving basally and tapering to bluntly rounded tip.

Distribution and habitat. The only known locality is the summit of Mt Aggie at ca. 1500 m, where according to the collector, "The site was in scrubby high altitude *Eucalyptus*, a few bits of snow were around and the ground was quite damp" (P.M. Johns, in litt.).

Etymology. Adjective, genitive singular, for the collector Peter M. Johns.

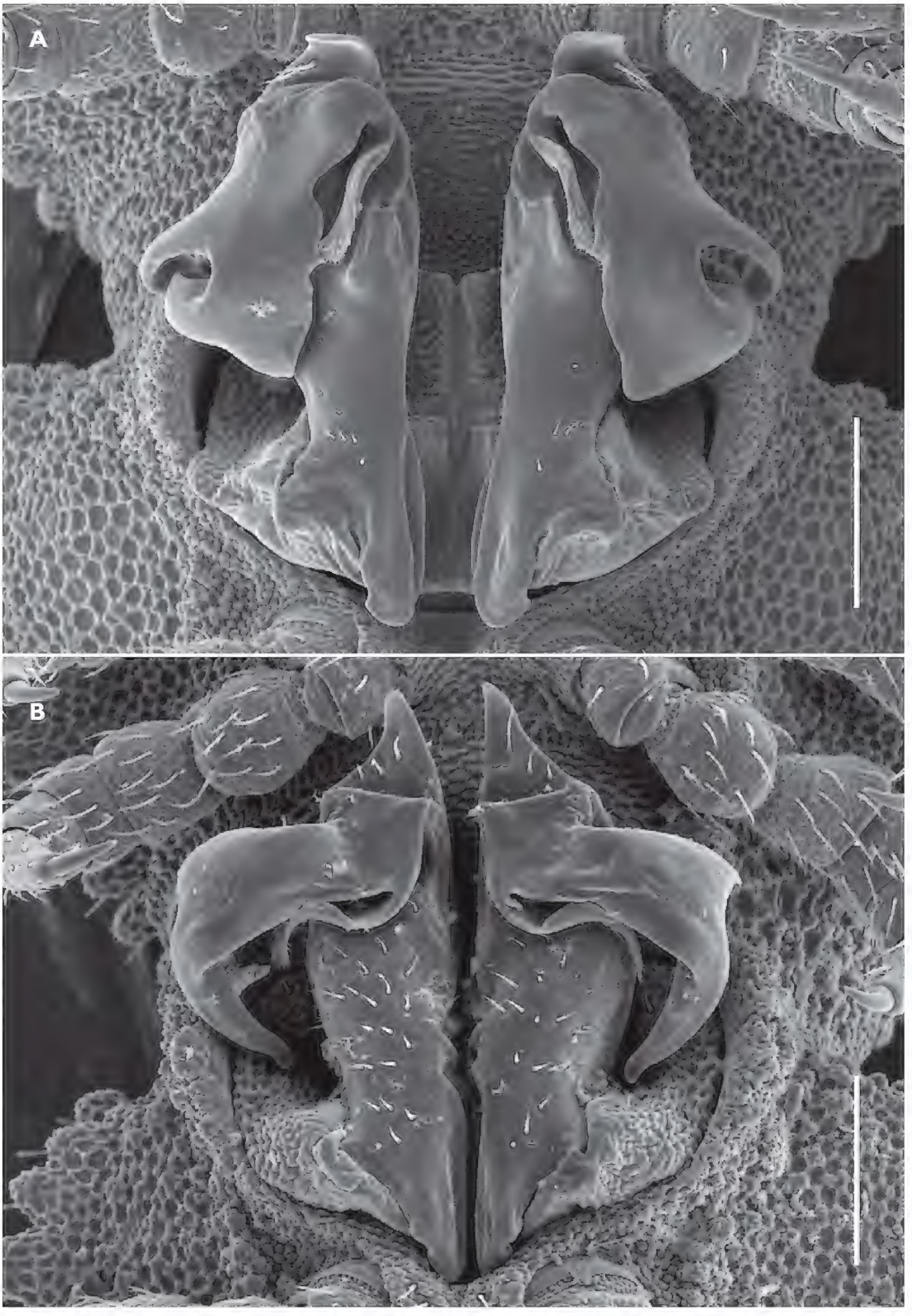

Figure 7. Ventral views of retracted male gonopods. **A** *Agathodesmus steeli* Silvestri, 1910, ex AM KS107964. **B** *Agathodesmus johnsi* sp. n., ex AM KS94156. Scale bars = 0.1 mm.

Discussion

Identification of *A. steeli*

The *A. steeli* type is mounted on its side and has evidently degraded over 100 years; not all of its characters are clearly visible. However, the type agrees with adult Knights Hill females in size, number and shape of rings, orientation of head and telson, and sizes and shapes of antennomeres and podomeres. More importantly, both the type and the Knights Hill specimens have variably sized tubercles with microsculpture, bisegmented setae, 5-6 large tubercles edging the ring 2 tergite (Figs 3A-C) and paranotum-like, four-tubercle lateral extensions on rings 3-18.

The Knights Hill specimens are clearly in the same genus as the type. It is still possible that they are not conspecific with *A. steeli*, which was collected ca. 20 km to the west in forest habitat lost many years ago. If the Knights Hill form also occurs in the remnant forests south and west of Avoca, where so far no *Agathodesmus* specimens have been found (Fig. 2C), I would be more confident in its identification with *A. steeli*.

It is curious that Silvestri (1910; see Appendix) noted setae arising laterally in the type, but did not record the more obvious fact that the lateral extensions and the ring 2 tergite have lobed margins.

Agathodesmus and *Atopogonus* as synonyms

As indicated in the *Agathodesmus* diagnosis (above), *A. johnsi* and *A. steeli* share several non-genitalic apomorphies with the two species described under *Atopogonus.* All four species also have inconspicuous ozopores located in non-tuberculated 'clear' zones low on the metatergites (Fig. 4B; Fig. 24 in Carl 1926; Jeekel 1986, p. 47). The most striking similarities, however, are in details of gonopod telopodite structure, as seen in Figs 8A-8E. These include a rounded terminal tab on the basal portion with three long setae on the posterolateral surface, and the division of the distal portion by notches into lobes in *A. baccatus*, *A. bucculentus* and *A. steeli*. The similarity in telopodite structure of the last two species is particularly striking (compare Fig. 7A with Figs 8D and 8E), and justifies placing them in the same genus.

Like *Agathodesmus*, the pyrgodesmid genus *Poratia* Cook and Cook, 1894 contains species with either 19 or 20 body rings (Golovatch and Sierwald 2001). Adis et al. (2001) suggested that the 19-ringed *Poratia digitata* (Porat, 1889) form could have evolved by neoteny from a larger, 20-ringed ancestor. Similarly, the 19-ringed ancestor of the miniscule *A. johnsi* and *A. steeli* might have evolved from a 20-ringed lineage represented today by the larger *A. baccatus* and *A. bucculentus*.

Family placement of *Agathodesmus*

Carl (1926) assigned his *A. baccatus* to Rhachidesmidae Carl, 1903. The remarkable lack of both a cannula and a prostatic groove inspired Verhoeff (1941) to establish Atopogonidae Verhoeff, 1941 for this species within the superfamily Rhachidesmidea Verhoeff, 1941, which also included Rhachidesmidae. Hoffman (1980) regarded *Atopogonus* as a genus of uncertain family position within the suborder Polydesmidea, but Jeekel (1986) placed it in Haplodesmidae. Hoffman (1999) agreed, but nevertheless felt that "the gonopods present a singular and highly disjunct pattern that invites taxonomic recognition at a level no less than subfamily (or family)" (p. 483). Golovatch et al. (2009) were unwilling to distinguish *Atopogonus* in this way, and listed it as one of six genera in Haplodesmidae after a careful revision of the family.

Here I follow Golovatch et al. (2009) in leaving *Atopogonus*, now synonymised with *Agathodesmus*, in Haplodesmidae. A haplodesmid character state demonstrated here for *A. johnsi* and *A. steeli* is bisegmentation of setae on the tergites (Golovatch et al. 2009); whether the other two described species in the genus have bisegmented setae is yet to be determined.

The *Inodesmus* problem

The name *Agathodesmus* may fall into synonymy with *Inodesmus* Cook, 1896 if "an intriguing and very difficult problem" (Hoffman 1999, p. 483) can be resolved. The problem has been briefly discussed by Jeekel (1986) and Hoffman (1999). Here I explore the problem in more detail.

In his self-published journal *Brandtia*, O.F. Cook added the new genus *Inodesmus* to Comodesmidae Cook, 1896 with the following words (Cook 1896b, p. 25):

> *From a cave in Jamaica I have specimens of a genus related to* Comodesmus.
>
> *Genus* Inodesmus, nov.
>
> *Differing from* Comodesmus *in the somewhat more slender, moniliform body, obsolete carinae, more projecting last segment, and normal pore-formula, the pores located in shallow depressions in the lateral middle of the segments, not in front of the middle as in* Comodesmus. *The only known species,* I. jamaicensis, *is about equal in size to* Comodesmus lanatus, *and is lighter brown in color, but may be faded.*

Since Cook assigned *Inodesmus* to Comodesmidae Cook, 1896 and compared it with the the type species of *Comodesmus* Cook, 1896, it is worth examining what Cook wrote about these taxa. I have corrected minor spelling and typographical errors in the following extracts:

Family Comodesmidae, new.

The type of this family is a small, reddish-brown, subcylindrical form, very rare, and also inhabiting the denser parts of the forest [in Liberia]. *The pore formula is unique: 5, 7, 9, 12, 15, 17, 18. The pores are located in the front part of the posterior subsegments. The dorsal surface is beset with conic piliferous granules, giving a woolly appearance. The last segment is scarcely produced beyond the anal valves, but is rounded off at apex as in many Iulidae. The head is not concealed by the first segment, which is narrower than the second and somewhat included between the carinae of the latter, much as in* Scytonotus granulatus *(Say).* (Cook 1896a, p. 415)

Comodesmus lanatus.
Antennae distinctly clavate; last segment decurved, the immediate apex small, projecting, truncate; lateral carinae present only as a longitudinal row of large tubercles, above which the tubercles are gradually smaller; length 8 mm., width 1 mm. (Cook 1896c, p. 258)

The location of the types of *I. jamaicensis* Cook, 1896, if they still exist, is not known. It is particularly ironic that the types may have been lost, considering that Cook understood the value of type specimens:

The importance of preserving type specimens with special care is now recognized throughout the scientific world, and where specific types are lacking, naturalists are endeavoring to supply their place by specimens collected in the original localities. This may be taken as a general admission of the obvious fact that purely descriptive methods are generally insufficient for scientific accuracy and need to be supplemented by actual specimens if correct identifications are to be permanently assured. (Cook 1900, p. 481)

Nearly 40 years after the establishment of *Inodesmus*, H.F. Loomis (1934) described another species in the genus from a set of females collected in Dutch Guiana (now Suriname). At the same time Loomis synonymised the monotypic *Lasiodesmus* Silvestri, 1908 with *Inodesmus*. There were now three species in *Inodesmus*: *I. jamaicensis* (Jamaica), *I. peduncularis* Loomis, 1934 (Suriname) and *I. caraibicus* Silvestri, 1908 (Puerto Rico). Discussing the new synonymy, Loomis wrote

After comparing the present species, from a generic standpoint, with Silvestri's description of Lasiodesmus *and with the brief characterization of* Inodesmus *Cook, there appears to be no reason for maintaining Silvestri's genus... The question of the distinctness of* Inodesmus jamaicensis *Cook and* I. caraibicus *(Silvestri) cannot be decided until comparison is made of the types or of specimens undoubtedly similar to the types.* (Loomis 1934, p. 65)

It seems clear from these statements that Loomis had not examined the types of *I. jamaicensis*. He was confident that his *I. peduncularis* and *L. caraibicus* were conge-

neric, because he had specimens of the former and a clear, beautifully illustrated description of the latter (Silvestri 1908). However, he was also confident that both were congeneric with *I. jamaicensis*, for which he had neither specimens, nor illustrations, nor an adequate description.

Thirty years later Loomis (1964) added another species to the genus, *I. globulosus* Loomis, 1964 from Panama, with only minor differences distinguishing it from *I. peduncularis*.

It is not clear whether Cook (1896b) had examined males of *I. jamaicensis*, but we know from the original descriptions that the three species assigned by Loomis to *Inodesmus* were based on all-female samples. In the late 1960s, samples of *Inodesmus* spp. including males were collected by Stewart Peck in Jamaica and Panama. The Jamaican millipedes, from two caves, were identified by Loomis (1969) as *I. jamaicensis* and redescribed. The gonopods of the Jamaican species were very different from those of the males collected by Peck in Panama and identified by Loomis as *I. globulosus*, so Loomis (1969) transferred the latter species to a new genus, *Hypsoporus* Loomis, 1969.

There is no evidence that Loomis compared the new Jamaican specimens with types of *I. jamaicensis*, but he was confident that they were conspecific:

> *Also present* [in the Peck collection] *were both sexes of the genotype species,* Inodesmus jamaicensis*, which O.F. Cook (1896) diagnosed very briefly in erecting the genus and which species has not been reported since.* (Loomis 1969, p. 141)

> *The exceedingly brief description of this species, its type locality given merely as "a cave in Jamaica," failed to mention many of the following characters which are of importance.* (Loomis 1969, p. 144)

The other two *Inodesmus* species, *I. caraibicus* and *I. peduncularis*, have since been shown to be synonyms, like *Hypsoporus globulosus*, of the pantropical "tramp" species *Cylindrodesmus hirsutus* Pocock, 1889 (Golovatch et al. 2001). The question remains: did Loomis (1969) describe Cook's *I. jamaicensis*, or a species in a different genus?

The descriptions of *I. jamaicensis* by Cook and Loomis agree only in body length (8-9 mm) and in the position of the ozopore (near the transverse midline of the metazonite). If we assume that Cook's *I. jamaicensis* shares with his *Comodesmus lanatus* those features not said to be different, then Cook's *I. jamaicensis* appears to agree with Loomis' *I. jamaicensis* in having the dorsal surface covered with more or less conical tubercles bearing long setae, and in having the paranota of ring 2 extending slightly forward. It does not seem enough on which to base an identification, and the fact that both came from Jamaican caves is hardly relevant, since Loomis (1969) says that his specimens have no "modifications indicating restriction to cave life" (p. 141), and Cook's specimens were pigmented.

The identity question became important when it was recognised by C.A.W. Jeekel that the gonopod of Loomis' *I. jamaicensis* (Fig. 8F) closely resembled that of the two *Atopogonus* species: "it is quite obvious that *Inodesmus jamaicensis* sensu Loomis, 1969,

is a species congeneric with *Atopogonus baccatus* and the presently described species [*A. bucculentus*]" (Jeekel 1986, p. 46). However, Jeekel (1986) was not convinced that Loomis had redescribed *I. jamaicensis*, and he refrained from synonymising *Atopogonus* with *Inodesmus*.

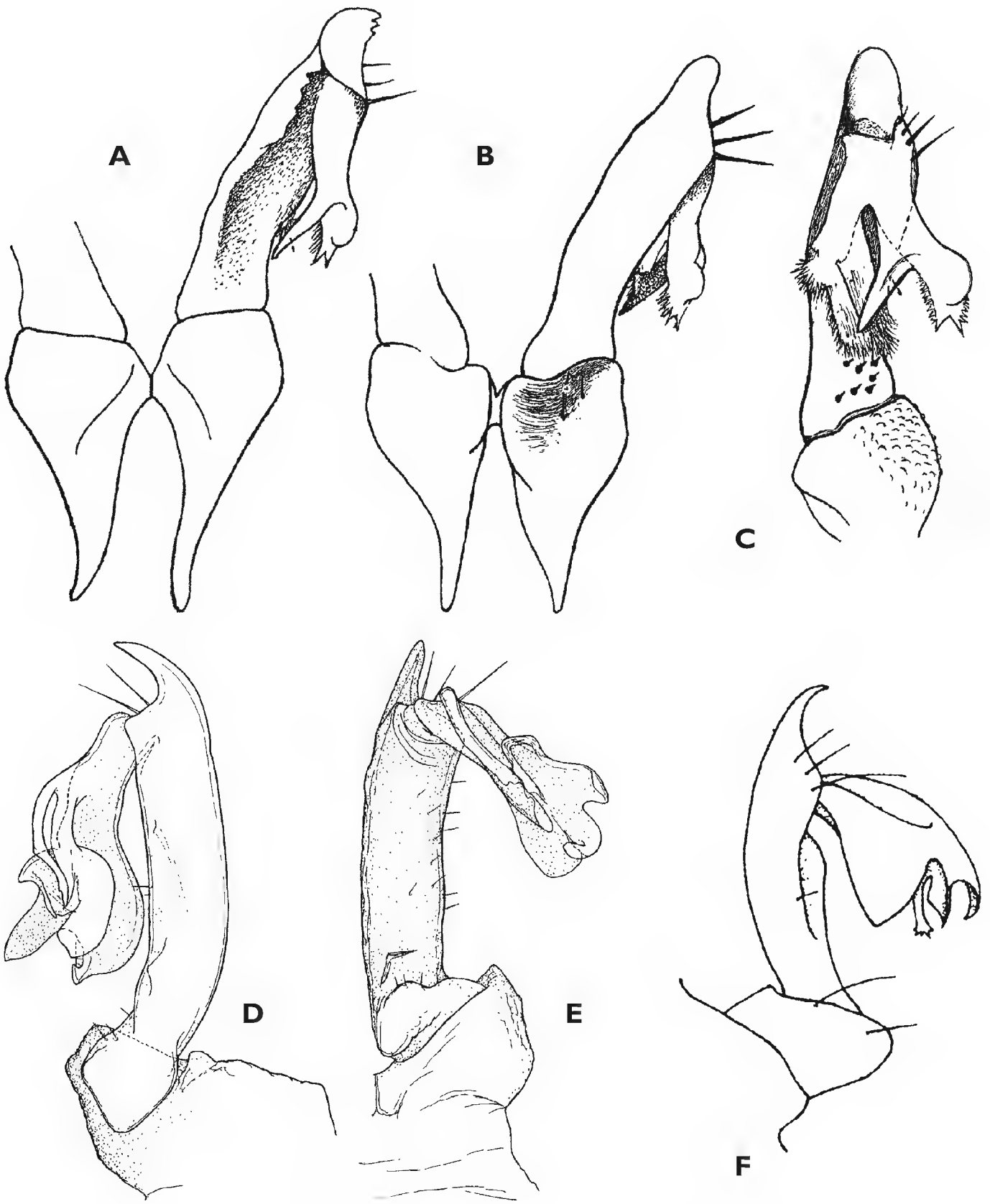

Figure 8. Gonopod drawings. **A-C** *Agathodesmus baccatus* (Carl, 1926) comb. n., Figs 26-28 from Carl (1926); **A** posterior view with left telopodite detail, **B** anterior view with right telopodite detail, **C** left telopodite, posterolateral view. **D**, **E** *Agathodesmus bucculentus* (Jeekel, 1986) comb. n., Figs 16 and 17 from Jeekel (1986), reproduced with permission; **D** right gonopod, medial view, **E** left gonopod, posterior view. **F** *Inodesmus jamaicensis* Cook, 1896 sensu Loomis, 1969, Fig. 7 from Loomis (1969); right gonopod, lateral view.

R.L. Hoffman (1999) was also unconvinced by Loomis' identification. Further, he was puzzled by the geographic disjunction between Australian and New Caledonian *Atopogonus* and Jamaican *Inodesmus* sensu Loomis, 1969. Jeekel (1986) had suggested that the genus was "in essence...a continental Australian taxon" (p. 46) which might have been carried by humans to New Caledonia and Jamaica. Hoffman (1999) reported that there was a second, undescribed species of *Inodesmus* sensu Loomis, 1969 in Jamaica's Blue Mountains rainforest, and argued: "While a multiple transport of rare and localized species from the Antipodes to a single West Indian island is not impossible, it does appear improbable. How else, then, can this distribution be accounted? If natural, it can only represent an astonishing case of reliction of a formerly widespread parental lineage." (p. 483).

If Cook's *I. jamaicensis* types are indeed permanently lost, then *I. jamaicensis* sensu Loomis, 1969 could be renamed as a species of *Agathodesmus*, leaving *Inodesmus* as a nomen inquirendum. Alternatively, it could be assumed that Cook's types are lost and that Loomis' identification is correct. A neotype of *I. jamaicensis* Cook, 1896 could then be selected from among the specimens examined by Loomis (1969), as suggested by Golovatch et al. (2009), and *Agathodesmus* would become a junior subjective synonym of *Inodesmus*.

A third and more satisfying possibility would be to first make a thorough inventory of Jamaican Polydesmida, both in and out of caves. If it could be shown that the only Jamaican genus fitting Cook's description is the one represented by the species described by Loomis (1969), then the three known *Agathodesmus* species should be moved into the older genus *Inodesmus*. I suspect, however, that there are other genera of small Jamaican Polydesmida with dorsal tuberculation and an anteriorly extended ring 2 tergite, and it is possible that Cook (1896) may in fact have redescribed *Cylindrodesmus hirsutus* as *I. jamaicensis*.

In this paper I leave the *Inodesmus* problem unresolved.

Key to described species of *Agathodesmus* Silvestri, 1910

1	Head + 19 rings **2**
–	Head + 20 rings **3**
2	Gonopod telopodite with broad lateral branch of distal portion apically expanded, notched and curving anterobasally (Avoca area, New South Wales, Australia) ..... ***Agathodesmus steeli* Silvestri, 1910**
–	Gonopod telopodite with broad lateral branch of distal portion tapering to apex, without notches and curving basally (Brindabella Ranges, New South Wales, Australia) ..... ***A. johnsi* sp. n.**
3	Body width ca. 2 mm; distal portion of telopodite with toothed fringes; New Caledonia ..... ***A. baccatus* (Carl, 1926) comb. n.**
–	Body width <1 mm; distal portion of telopodite without toothed fringes; Queensland, Australia ..... ***A. bucculentus* (Jeekel, 1986) comb. n.**

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Appendix

Original description of *Agathodesmus steeli* from Silvestri (1910), pp. 362-363, with translation.

8. Gen. *Agathodesmus* nov.

(F) Corpus capite, collo, segmento anali et segmentis aliis 18 constitutum, longum, subcylindraceum, postice paullulum angustatum, carinis minimis, dorso tuberculis parvis, lateraliter breviter setigeris, instructo, in spiram contractile.

Caput manifestum, ab antennarum radicibus ad marginem externum fovea transversali excavatum, clypeo in parte postica laterali aliquantum inflato et tuberculis aucto.

Antennae breviores, articulo sexto quam ceteri multo longiore et crassiore.

Collum subellipticum, convexum, caput latitudine subaequans.

Trunci segmentum primum metazonae lateribus quam carinae segmentorum sequentium multo longioribus et latioribus, antrorsum extensis et late rotundatis.

Carinae minimae, parum supra ventris libellam orientes, transversales.

Pori in segmentis 4, 6, 8, 9, 11, 12, 14-17 (= 5, 7, 9, 10, 12, 13, 15-18 Auct.), in parte mediana laterali segmentorum, sat longe a carinarum margine laterali, sese aperientes.

Segmentum praeanale lateraliter utrimque sinuatum, parte postica crassa, apice truncato valvulas anales paullulum superans.

Sterna inter pedum basim valde angusta. Pedes breviores, articulo secundo quam tertus parum longiore.

Mas latet.

Typus:

Agathodesmus steeli sp. n.

Subochraceus.

Long. corp. mm 6, lat. segmenti noni cum carinis 0,60, sine carinis 0,46; long. antennarum 0,54, pedum 0,45.

Habitat: Avoca (Nova Hollandia: N.S. Wales. Thomas Steel legit).

8. Gen. *Agathodesmus* nov.

(F) Body composed of head, collum, anal segment and 18 other segments, long, subcylindrical, a little narrowed posteriorly, keels very small, dorsally with small tubercles, laterally with short setae, curling spirally.

Head distinct, excavated from the antennal base to the outer margin with a transverse pit, clypeus a little inflated posterolaterally and provided with tubercles.

Antennae quite short, sixth article much longer and thicker than others.

Collum subelliptical, convex, subequal to head in width.

Sides of first trunk segment metazona much longer and wider than keels of subsequent segments, extended anteriorly and broadly rounded.

Keels very small, arising just above the level of the venter, transverse.

Pores in segments 4, 6, 8, 9, 11, 12, 14-17 (= 5, 7, 9, 10, 12, 13, 15-18 of other authors), opening in median lateral portion of segments, some distance from the lateral margin of the keel.

Preanal segment sinuous on both sides, posteriorly inflated, apex truncate, extending a little past the anal valves.

Sternites between leg bases very narrow. Legs short, second article just longer than third.

Male unknown.

Type:

Agathodesmus steeli sp. n.

Almost ochre-coloured.

Body 6 mm long, segment 9 0.60 mm wide with keels, 0.46 mm without; antenna 0.54 mm long, leg 0.45 mm.

Habitat: Avoca (New Holland: N.S. Wales. Collected by Thomas Steel).